Changes in Gastropod Ecology in Response to the Formation of the Isthmus of Panama

Undergraduate Research Thesis

Submitted in partial fulfillment of the requirements for graduation

with research distinction in Earth Sciences

in the undergraduate colleges of

The Ohio State University

By

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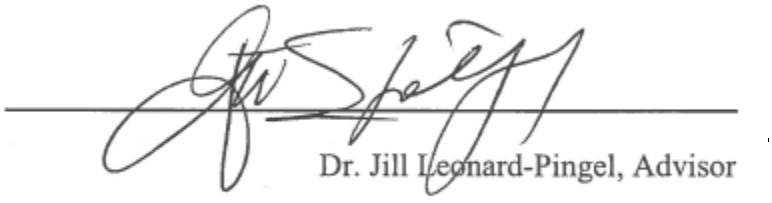
The Ohio State University

2018

Approved by



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Abstract

Changes in the relative abundance of gastropod genera in the southwest Caribbean over the past 10 Ma were documented to determine their response to oceanographic changes brought about by the emergence of the Isthmus of Panama and closure of the Central American Seaway 3.5 Ma. Bulk samples from 25 localities yielded 1757 samples, 16,121 identified specimens and 54 distinct families. All specimens from the same locality were assigned to a faunule that was associated with a specific time. The composition of faunules based on quantitative data for feeding habits revealed strong shifts in community structure, with stark contrast between faunules older than 5ma and those younger than 3.5 Ma. These changes are primarily due to shifts in the feeding habits of the gastropods. Taxa with preferential feeding associated with rocky or coral substrates increased in abundance while taxa associated with soft substrate environments decreased in abundance but did not disappear entirely. The results support other research that indicates increases in coral reefs and shallow rocky environments were important drivers of biologic changes in the Caribbean shallow seawater communities. By studying the biologic turnover of gastropods in the Caribbean the causes of changes to benthic communities in response to large scale ecological shifts can be better understood.

Acknowledgements

I would like to thank my advisor Dr. Leonard-Pingel for her guidance and support throughout this project. I'd also like to extend thanks to Molly Hunt for helping with sample organization and data entry. I'm also grateful to Dr. Carey for her guidance during this daunting process. The School of Earth Sciences here at The Ohio State University has provided me with all I needed to learn and grow into a proper scientist and for that I'm extraordinary thankful. Thank you to Mike and Cindy Morgan for their incredible Field Experience Travel Fund that allowed me to experience Ohio State's field camp. I'd also like to extend a huge thank you to Mr. Zender, my high school science teacher who introduced me to geology and opened my mind up to exploring a career in the STEM field. I'm also grateful for all my friends and roommates that helped me push through the tough times and provided me words of encouragement. To my older brothers, Chris, Steve and Kurt, I'm immensely thankful. I learned a great deal from watching you guys grow up and wouldn't be where I'm at without you guys. To my parents, I don't think I could ever string a series of words together to express just how appreciative I am for all that you've done for me and your continued love and support keeps me striving to better myself every day.

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Introduction

Background Information

The Panama arc began as a volcanic arc approximately 73 Ma as the Caribbean plate moved eastward arriving at its current position by approximately 50 Ma (O'Dea et al., 2016). While this was occurring the North and South American plates continued to move westward past the Caribbean plate causing a strike slip motion in the east-west direction (O'Dea et al., 2016). In addition to the strike-slip motion the South American and Caribbean plates began to converge in a north-south direction that lead to the collision of the Panama Arc with South America. This collision drove uplift in both the Northern Andes and the Panama block, forming the North Panama Deformed Belt and closing the Central American Seaway and ultimately forming the Isthmus of Panama approximately 3.5 Ma (O'Dea et al., 2016). The formation of the land bridge meant Pacific and Atlantic waters would no longer intermix. Furthermore, the emergence of the Isthmus brought about changes to the Westerly Trade Winds which in turn caused increased evaporation over the Caribbean (Lunt et al., 2007). The increased evaporation and lack of intermixing of the ocean waters caused the Caribbean waters to become saltier with Caribbean and Pacific Ocean salinity levels diverging from each other starting around 4.6 Ma and reached modern levels 4.2Ma (O'Dea et al., 2016). Also, isolation from the El Nino events caused a loss in seasonal variations of temperature and productivity in the Caribbean. An extinction event followed the emergence of the Isthmus affecting all major marine taxa in the Caribbean and western Atlantic with taxa associated with benthic environments hit especially hard (O'Dea et al, 2007). The exact reasons the extinction occurred are still unknown, however there is consensus that the changes in productivity, and subsequent changes in benthic habitats, had some effect. The emergence of the Isthmus of Panama caused oceanographic changes that drove biologic changes in the Caribbean. A study of changes in marine taxa should lead to a better understanding of the drivers of biologic changes and thus a better understanding of the relationship between environment, ecology and taxonomic turnover can be examined.

Hypotheses

To enhance the understanding of the relationships among environment, ecology and taxonomic turnover the question of environmental cause and effect for changes in communities of gastropods were examined. To approach this question the relative abundance and dietary habits of gastropods samples from the Caribbean were evaluated. Work with bryozoans and scallops in the area strongly suggest that the decrease in productivity was the primary factor driving taxonomic changes in the Caribbean, however the causes of changes in other taxonomic groups is complicated by a 1-2 Myr time lag between the onset of environmental changes and community changes in the Caribbean (O'Dea et al., 2007). Overall, there was a shift in benthic ecosystems from heterotrophic mollusks to mixotrophic reef corals, calcareous algae and shallow water seagrass meadows. These changes correspond well with a simple model of decreased upwelling and productivity caused by the closure of the Central American Seaway (O'Dea et al., 2007). However, extinction rates of mollusks and corals did not increase until 3-2Ma and peaked between 2 and 1 Ma, even though the turnover event affected taxa associated with high

productivity the most (O'Dea et al., 2007). This suggest that something else other than the productivity change alone was involved in community changes. By comparing the taxa that survived the late Pliocene extinction event against those that became extinct expands the understanding of likely causes of the taxonomic turnover. The hypotheses that have emerged, from associated research, suggest the causes for community changes in the Caribbean have been driven by two interdependent factors: decreases in productivity and increased development of coral reefs and shallow water seagrass meadows. These hypotheses were tested through quantitative study of changes in gastropod ecology in response to environmental change. First, the decrease in planktonic productivity should be accompanied by a decrease in suspension-feeding gastropods as they are most correlated with planktonic activity. Second, an increase in coral reef and seagrass environments should be accompanied by an increase in specimens that preferentially feed on corals or rocky substrates and those that feed on plants. In contrast the increase in reef and seagrass environments and subsequent loss of soft muddy substrate environments, should coincide with a decrease in the abundance of predatory gastropods as their prey was affected by changing productivity. Overall the changes in productivity and benthic ecosystems should have caused an increase in the diversity of gastropod taxa present and for more diverse feeding habits to develop. The results suggest changes in gastropod life habits were directly influenced by changes in the environment and benthic habitats.

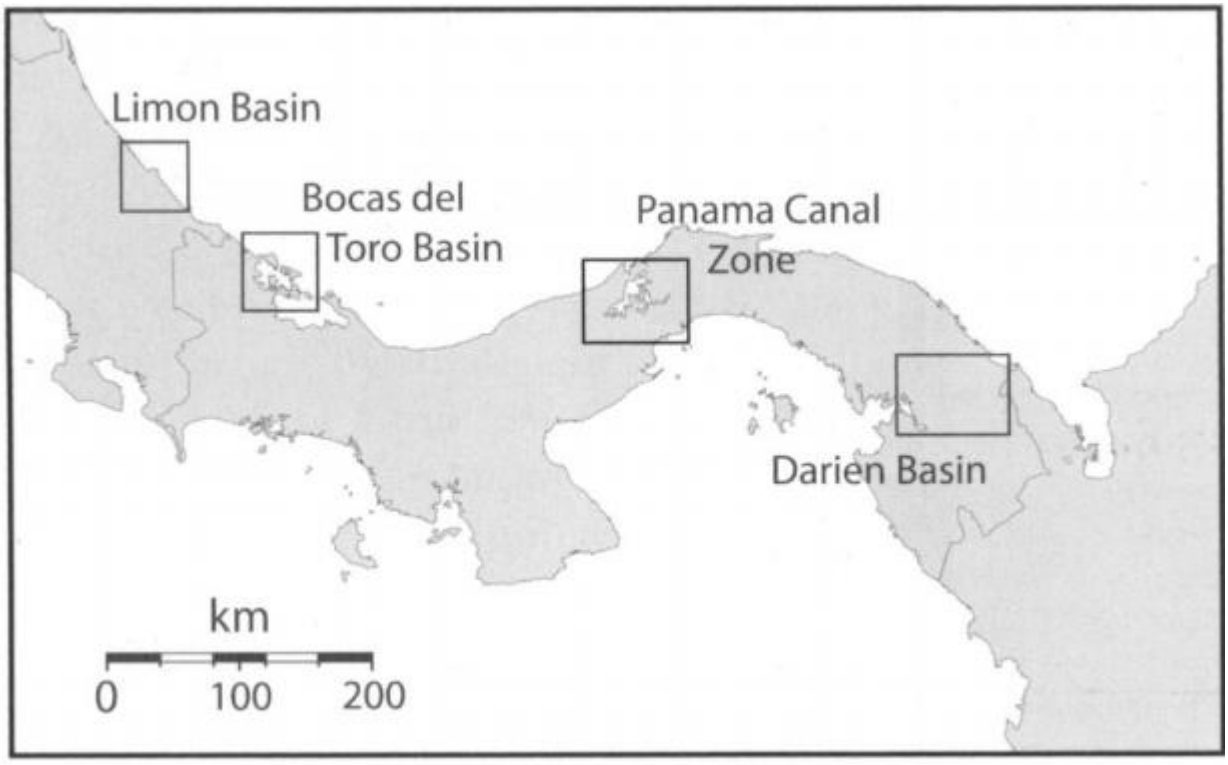

Figure 1- Map of Panama and eastern Costa Rica showing the basis from which specimens were collected (image taken and adapted from Leonard-Pingel et al., 2012).

Methods

(i) Collection

Collections were made as part of the Panama Paleontology Project (PPP) and build on previous PPP studies of stratigraphy, age dating, paleoenvironments and faunal composition (Leonard-Pingel, Jackson and O'Dea, 2012). Collections were made in in the Limon Basin on the Caribbean shore of Costa Rica and from the Bocas del Toro, Darien, and Panama Canal Zone basins along the Caribbean coast of Panama. Samples from a single outcrop or adjacent exposures that could be assigned to the same age and environment were grouped into faunules. Faunules represent the best approximation of fossil communities (Leonard-Pingel et al., 2012). Age of the faunules were approximated by using stratigraphic position or ages inferred from previous studies (Leonard-Pingel et al., 2012). Time averaging, or temporal mixing of fossils, may result in mixing of the ecological signals, but it also increases the likelihood that a sample accurately represents an ancient community by dampening seasonal variations which ultimately provides a more complete picture of ancient gastropod assemblages (Kidwell and Flessa, 1995). The abundance of gastropod genera was measured from bulk samples. The bulk samples were repeatedly frozen and thawed in Glauber's salt solution. This process breaks down the sediment matrix while reducing damage to the fragile shells of the fossils (Surlyk, 1972) Specimens were sorted to class and the gastropod specimens were then sorted to the genus level. In general, the morphology of gastropod shells is much more complicated and poorly understood than that of bivalves, also, many gastropods have lifestyles in which their shell is less intimately associated with the substrate on or in which it lives (Todd, 2001). For this reason, analysis is focused on gastropod diets which can be more reliably assessed. (Taylor and Reid, 1984).

(ii) Analysis

Feeding habits of the gastropod samples were determined from the Neogene Marine Biota of Tropical America database (Todd, 2001). For many gastropod families all genera have the same feeding habit, but for some harder to study families' datum for a few species has been applied to the whole family. Grouping the specimens into faunules allowed for changes in gastropod taxonomy and ecologically throughout time to be analyzed. To overcome variance in the sample sizes of the faunules some analyses were done by combining the faunules into 3 different age groups. Data analysis methods include linear assessment through time of family richness (S), which was done by plotting the number of families of gastropods in a faunule against its associated time value. Shannon's Index of Evenness ((∑ (% abundance of specimens in family x * ln (abundance of specimens in family x))/ ln(S)) for each faunule was also plotted against associated ages. Shannon's Index of Evenness is a measure of biodiversity which quantifies how equal the faunule is numerically. Furthermore, Kruskal-Wallis tests and frequency diagrams were also created. Frequency diagrams were created by calculating the number of times each family had at least one specimen present in a faunule and was divided by the total number of faunules for that age group. For example, the predatory carnivorous family Nassariidae was found to have at least one specimen in 3 of the 4 faunules associated with ages before the closure of the Central American Seaway therefore it's frequency for that age group is .75. The Kruskal-Wallis test was done in MATLAB and is a non-parametric method for testing whether samples originate from the same distribution. It's useful for comparing two or more independent samples of different sample sizes and determines whether the medians of two or more groups are different.

Results

After evaluating the samples, 25 different faunules were identified with ages ranging from 9.6MA-.007 Ma. Table 1 summarizes the findings for each faunule along with number of different families and number of different feeding categories for each faunule.

Table 1: showing the name and age associated with each faunule along with number of sample and specimens for each. Number of different feeding categories and families was also calculated and presented in this table. *Represents the number of distinct possibilities.

Faunule Name	Age (Ma)	# of Samples	# of Identified specimens	# of Feeding Categories	# of Families
Isla Payardi (1)	9.6	164	3187	9	23
Mattress Factory (2)	9	30	180	5	13
Rio Indio (3)	6.95	29	83	3	10
Rio Tupisa (4)	6.35	43	262	5	17
Cayo Agua: Roja W. (5)	4.25	156	1539	11	31
Isla Popa (6)	4.25	34	93	3	13
Cayo Agua: Pt. Norte W. (7)	4.25	107	370	6	22
Cayo Agua: Pt. Norte E. (8)	4.25	26	99	2	5
Cayo Agua: Nispero (9)	3.55	20	198	4	8
Cayo Agua: Pt. Tiburon-Pt.Piedra (10)	3.55	15	72	2	5
Isla Solarte (11)	3.55	64	512	7	18
Rio Vizcaya (12)	3.55	39	1040	3	17
Santa Rita (13)	3.55	19	45	5	6
Quebrada (14)	3.1	15	257	6	12
Bomba (15)	3.05	177	1413	8	27
Fish hole (16)	2.6	13	87	2	5
Ground Creek Mud (17)	2.05	146	1427	9	26
Ground Creek Porites (18)	2.05	40	197	5	10
Wild Cane Key (19)	2.05	74	296	10	27
Wild Cane Reef (20)	2.05	38	335	4	10
Cemetary Pueblo Nuevo (21)	1.6	11	23	3	3
Empalme (22)	1.6	165	1481	9	35
Upper Lomas (23)	1.6	146	1636	5	15
Swan Cay (24)	1.4	50	548	7	16
Lennond (25)	0.007	136	741	12	31
		1757	16121	20*	49*

(i) Taxonomic Diversity Through Time

The largest age gap in the data is between 4.25-6.35Ma. The number of samples and specimens varied greatly between the individual faunules. The smallest sample size was for the faunule Cemetery Pueblo Nuevo(1.6Ma) with only 11 samples and 23 specimens and the largest being Isla Payardi (9.6Ma) with 164 samples and 3,187 specimens. The overall number of specimens is largely based on the density of the fossil deposits at the local they were taken from. Some formations include dense shell bed while others (like Cemetery Pueblo Nuevo) only preserves scattered shells, so it is much harder to get large number of specimens from some of the locations. Family Richness (S), which is simply the count of the number of different families in a faunule, was plotted against the time associated with the faunule. Figure 2 shows a slight increase in the number of families throughout time, however this may be affected by variance in the number of specimens per faunule. To evaluate how Family Richness (S) may be affected by variance in sample size the total number of specimens in each faunule was plotted against Family Richness (S). Figure 3 shows that faunules with higher numbers of families are also typically the faunules with higher numbers of identified specimens. Shannon's index of evenness was also plotted against time and shows little change.

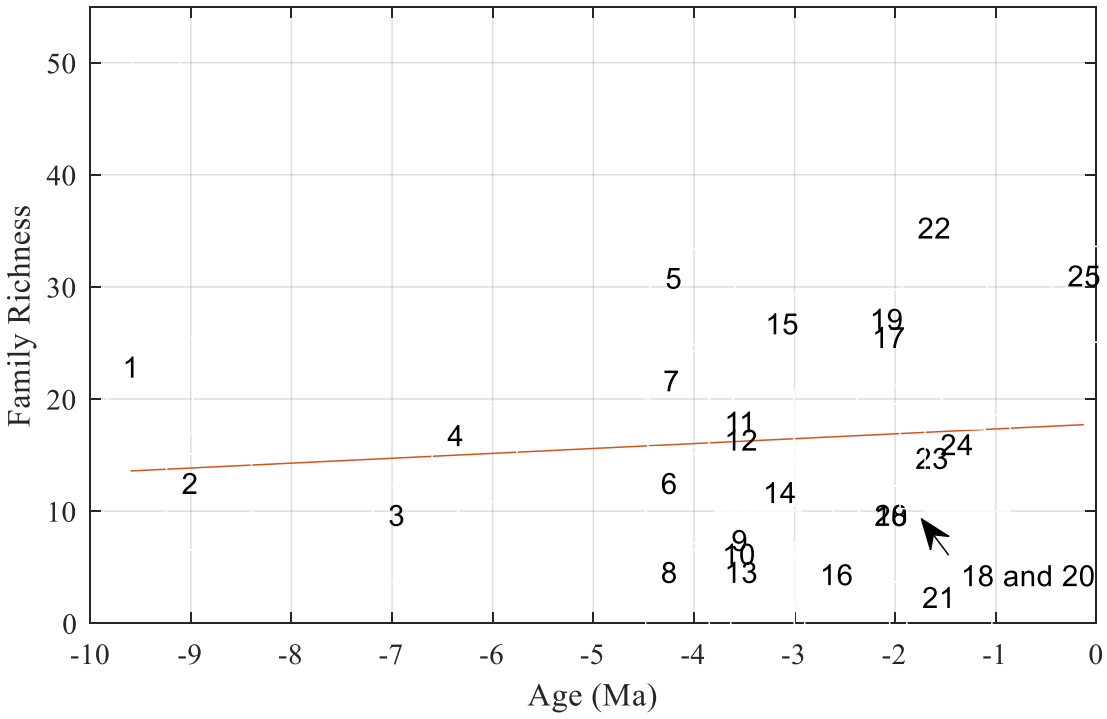

Figure 2: shows the Family Richness of each faunule plotted against the associated time for the faunule. The numbers are associated to a faunule presented in table 1. The dashed red line is a line of best fit.(R^2=.0115)

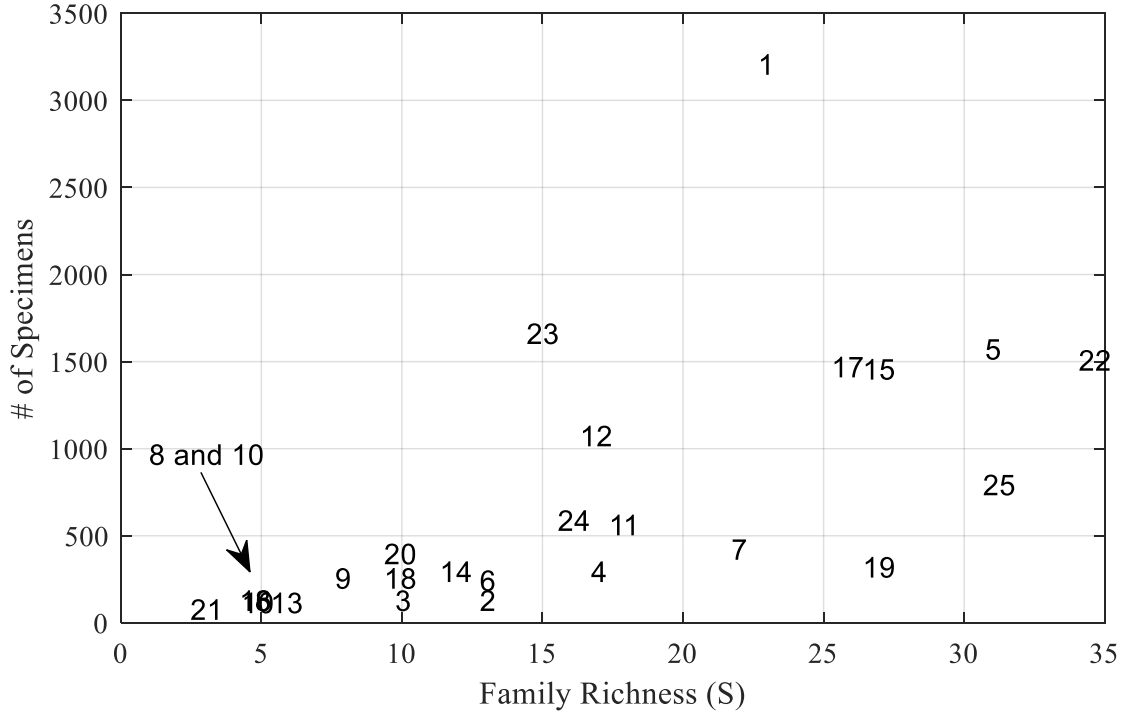

Figure 3- Showing Family Richness plotted against number of specimens for each faunules. Shows how the faunules with higher numbers of Family Richness are also the faunules with higher numbers of identified specimens. The numbers are associated to faunules in table 1

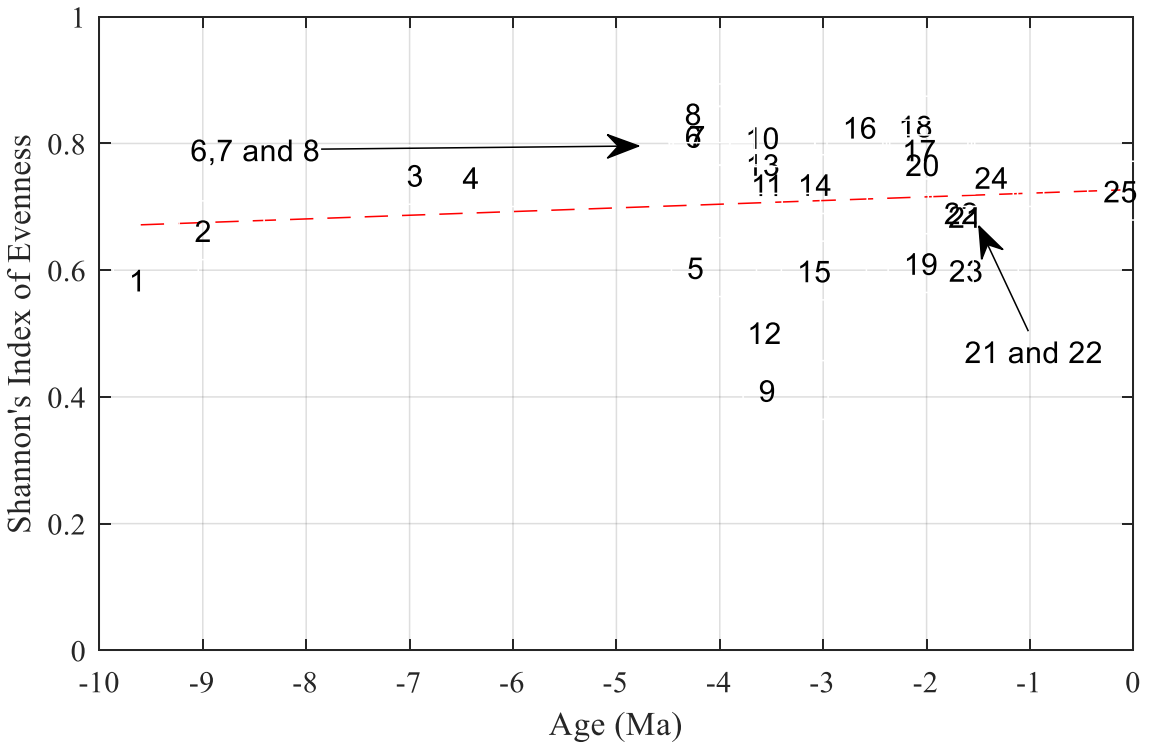

Figure 4: Show Shannon's Index of Evenness for each faunule plotted against the time associated with that faunule. The red dotted line is a line of best fit.(R^2=.0152). The numbers are associated with faunules in table 1.

A stock diagram showing the changes in frequency throughout time for the 54 Families identified in our data was created. Listed next to each family is the feeding activity that is associated with their family. Feeding habits are considered in terms of what types of food are eaten. For example, the family Turridae feeds on polychaetas (Sea worms) so they are categorized as Predatory Carnivores (CP), while specimens in the family Coralliophillidae feed on corals and other colonial animals so they are classified as browsing carnivores (CB).

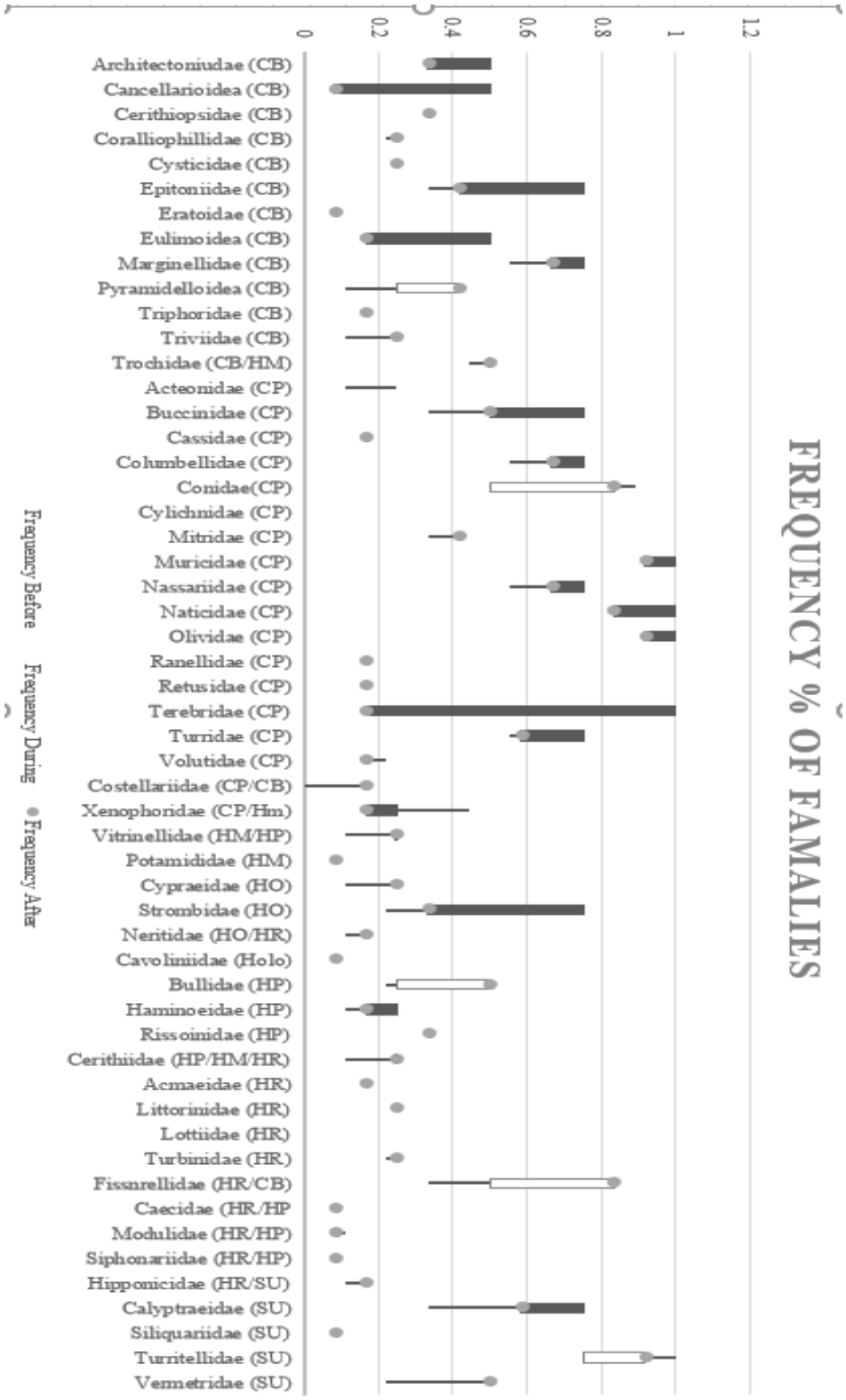

Figure 5- Stock bar graph showing the frequency changes of the specific families, the abbreviations in parentheses are the feeding habits associated with the family. Up/Down bars for the families found in all 3 age groups was added to highlight their specific changes.

(ii) Changes in Feeding Habits Through Time

Within the 54 distinct families identified there was a total of 17 feeding habits identified. The total number of distinct feeding habits per faunule was plotted through time and shows a slight increase in the number of feeding habits. To evaluate how the variance in identified specimens per faunule affected how many feeding groups were identified, total specimens in each faunule was plotted against the number of feeding habits for that associated faunule. Figure 7 implies that the higher numbers of identified specimens means higher numbers of feeding habits. However, there are some exceptions, for example, Lennond (.007Ma) has the highest number of feeding habits but has a relatively low number of identified specimens when compared to other faunules. Furthermore, Wild Cane Key has a higher number of feeding habits present compared to Isla Payardi (9.6Ma) despite having the large disparity in identified specimens. This suggests that although the number of feeding groups per faunule is affected by the number of specimens there is still a general increase seen in the number of feeding habits.

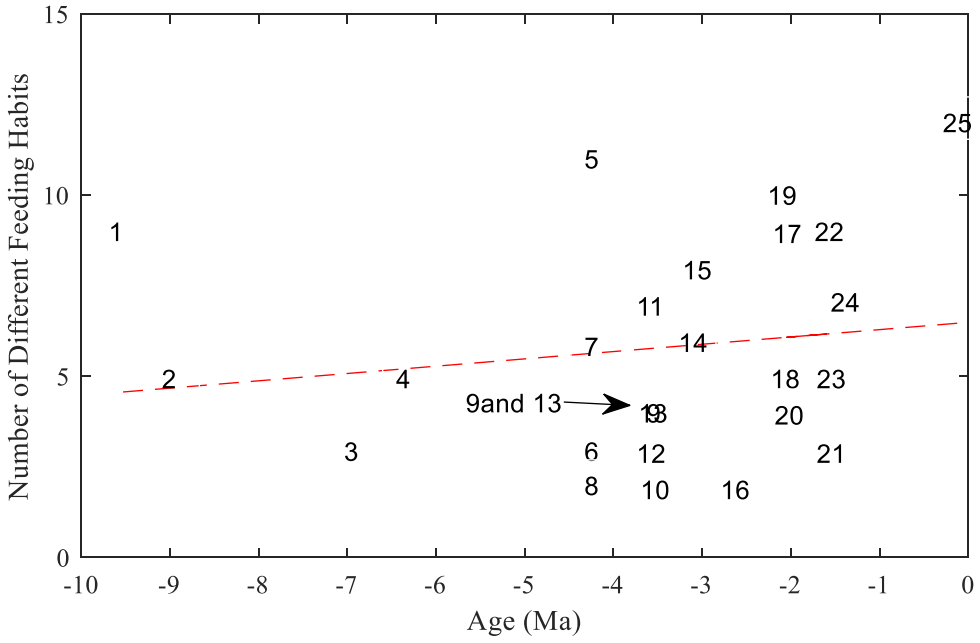

Figure 6- showing the number of different feeding groups for each faunule plotted against the age associated with it. The numbers correspond to the faunules listed in table 1. The red dotted line is a line of best fit. (R^2= .0245).

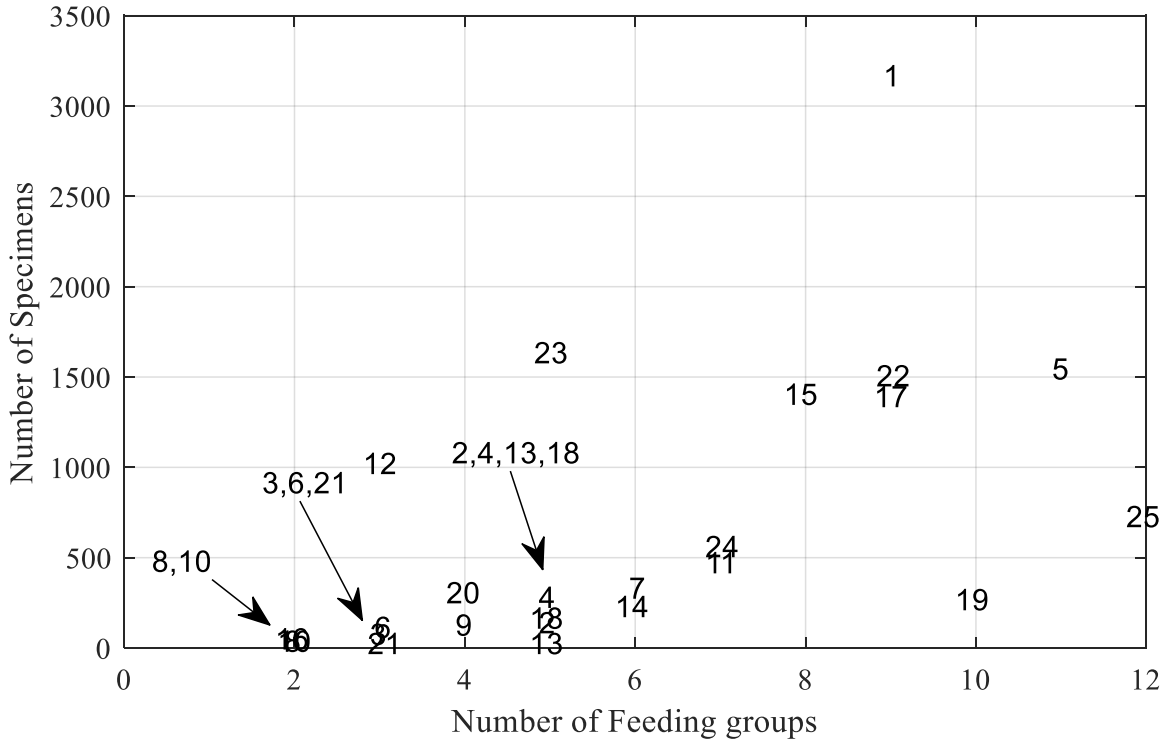

Figure 7- Number of feeding groups plotted against the number of specimens for each faunule. Shows how higher numbers of feeding groups is associated with higher numbers of specimens. The numbers are correlated to faunules in table 1.

To normalize sample sizes and increases the robustness of statistical tests, as well as decrease noise in samples, faunules were combined into 3 age groups that represent 3 stages in Isthmus formation. The 3 age groups vary in age from before (6.35-9.6Ma), during (4.25-3.55Ma) and after (3.1-.007Ma) the closure of the Isthmus of Panama. There is a total of 4 faunules in the before (6.35-9.6Ma) age group with a total of 3,709 identified specimens, in the during (4.25-3.55Ma) age group there are 9 faunules with a total of 3,968 identified specimens. In the After (3.1-.125Ma) age group there are 12 faunules with a total of 8,411 identified specimens. Of the 17 independent feeding habits, 7 main dietary habits were identified. These include Predatory Carnivores (CP), Browsing Carnivores (CB), Herbivorous Omnivores (HO), Herbivores on fine-grained substrates (HM), Herbivores on rock, rubble or coral substrates (HR), Herbivores on plant or algal substrates (HP) and Suspension Feeders (SU). Percent abundance was calculated for each main dietary habit for the faunules in the 3 age groups to gain a better understanding how each feeding habit changed during the formation of the Isthmus.

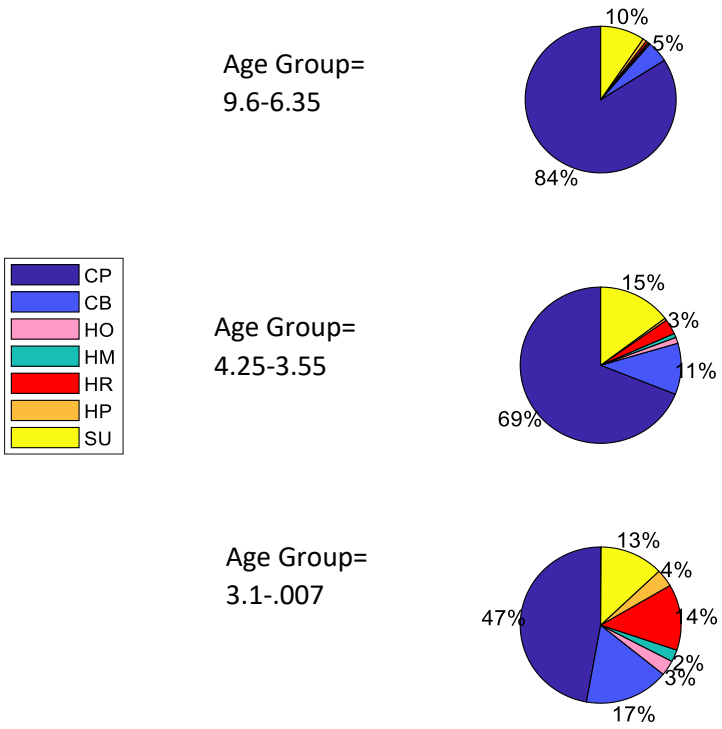

Figure 8- showing the percent abundance of the 7 main dietary habits for specimens in faunules for the 3 different age groups. Top is the faunules associated with times before (6.35-9.6) the closure of the Central American Seaway. Middle is for the faunules in the during age group (4.255-3.55). Bottom is for the faunules in the after-age group (3.1-.007)

(iii) Changes in Categorical Groups

To asses more general trends in feeding habits categorical groups were established. Specimens labeled as predatory gastropods, browsing carnivores or a combination of both were categorized as Carnivores. Specimens labeled as Herbivores Omnivores or had a combination of predatory behavior and herbivorous behavior were categorized as omnivores. Specimens identified as herbivores on soft substratum, or as herbivores on rock, rubble or coral substratum or as herbivores on plant or algal substratum were categorized as Herbivores. Suspension feeding specimens were left in their own separate category as their feeding habit is was the most unlike the others. The percent abundance of specimens identified to be one of the 4 categories was plotted against time to gain a greater understanding of how these feeding categories changed over time.

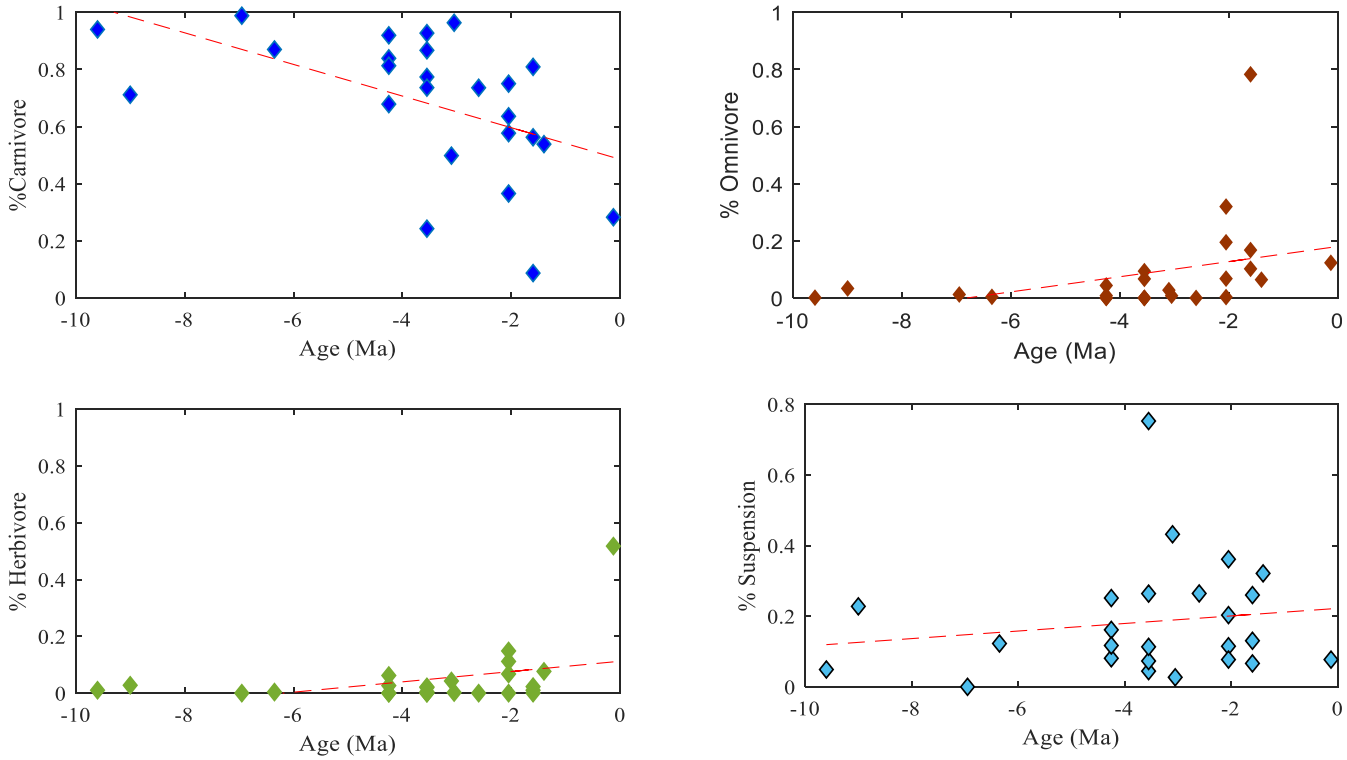

Figure 9- shows percentage abundance of specimens identified to be either Carnivores (Blue- Top Left) Omnivores (Red-Top Right), Herbivores (Green-Bottom Left) or Suspension (Light Blue-Bottom Left) feeders in the faunules plotted against the time associated with that faunule. Each diamond represents a faunule. Note the decreases in Carnivores but increases for all other groups. The red dotted lines are lines of best fit.

The percent abundance data for each of the feeding categories in each age group was submitted to a Kruskal-Wallis to test for changes in distribution. For carnivores a decrease of significant value was found across the 3 age groups while in contrast, increases of significant values was found for Omnivores and Suspension feeders. While Herbivores saw a slight increase the difference for the 3 age groups was found to be insignificant.

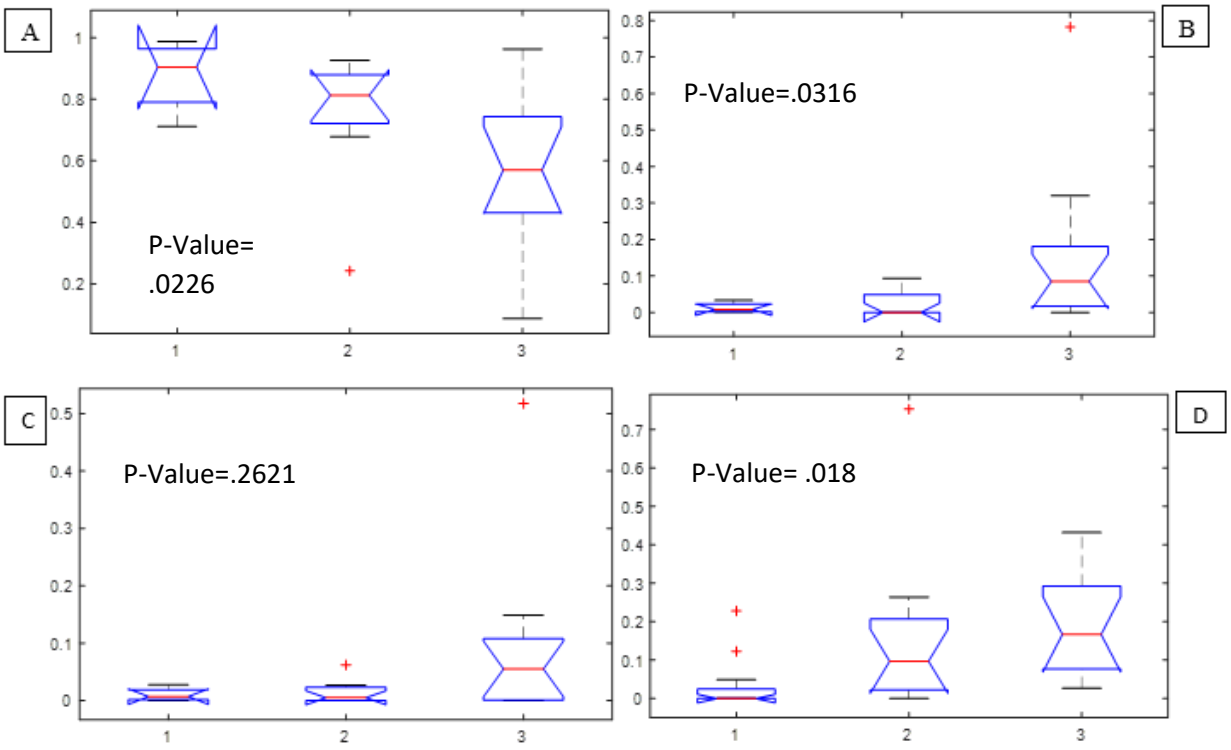

Figure 10- Shows the Kruskal-Wallis plots for A. Carnivores B. Omnivores C. Herbivores and D. Suspension feeders for the age groups 1. Before 2. During and 3. After (referencing timing to the emergence of Isthmus of Panama).

Discussion

Taxonomic and Functional Diversity

Analyses of faunules through time reveals shifts in community membership and diets in response to changing environmental conditions. Overall, diversity doesn't change a significant amount rather there are shifts in the families that were present. This observation is consistent with a pattern of origination and extinction at the species level (Jackson et al., 1999). In the faunules that are from before the Isthmus closed (9.6-6.35Ma) there are 26 families with at least one specimen present. 24 of those families have specimens present in faunules with associated ages during (4.25-3.55Ma) and after (3.1-.007Ma) the formation of the Isthmus. The 2 families not present in the later faunules are associated with carnivorous feeding habits. For faunules with associated ages during the formation of Isthmus there was an additional 11 families found to have at least one specimen and 16 families that were only present in faunules with associated ages after the formation of the Isthmus. Of the 16 families only present in faunules after the formation of the Isthmus 8 of them have herbivorous feeding habits. This pattern is consistent with the marked increase in Caribbean reef and shallow seagrass glade development in the late Pliocene and Pleistocene (O'Dea et al., 2007) Overall there was an increase in the family richness of the faunules throughout time. This observation in consistent with other research done in the Caribbean that shows increases in diversity of other mollusk groups such as the Bivalves (Leonard-Pingel et al., 2012).

Changes in Feeding habits

The environmental changes that were brought about from the closure of the Central American Seaway allowed reef-building corals and other colonial animals to multiply. This coupled with decreases in seasonality and areas with higher planktonic activity due to terrigenous runoff means the Caribbean coastal environments are much more heterogenous than the Pacific (O'Dea et al., 2007). Decreases in seasonal variations caused by the closure of the Central American Seaway had marked effects on productivity and habitats of benthic environments in the Caribbean which in turn influenced the feeding habits of the different categorical feeding groups of gastropods.

(i) Carnivores

The faunules older than 3.5Ma have higher frequency and abundances of the families Muricidae, Olividae and Naticidae. These families are predatory carnivores that feed on barnacles, polychaetas, other gastropods and even small fish (Hughes, 1986). Faunules younger than 3.5Ma show increases in frequency and abundances for the families Margenliidae and Architectoniudae which are browsing carnivores whose diets consist of feeding on colonial animals such as corals, cnidarians and sponges (Hughes, 1986). There are also examples of species that participate in both predatory behaviors, which also occurs more frequently in the younger faunules. Overall, there was a general decrease in the overall abundance of carnivorous specimens. The older faunules were consistently dominated by Carnivores while in the younger faunules, specifically the Lennond, Sway Cay and Upper Lomas faunules, there are significant decreases in the number of carnivorous specimens. Carnivorous gastropods are still dominant in those younger faunules however this is largely due to the increase in the number of Browsing Carnivores present as Predatory Carnivores saw a significant decrease. This observation is consistent with other research that shows predatory mollusks were especially affected by the environmental changes

associated with the emergence of the isthmus (O'Dea, 2007) However from my data most of the decline occurred 1.5-2My after the dramatic decline in seasonality suggesting the influence of other factors in the decline of predatory mollusks. The changes in benthic environments after the closure of the Central American Seaway likely influenced prey species available for predatory gastropods. Before the closure, predatory gastropods likely patrolled deep water sea grass meadows (relatively deep, all samples come from a paleodepth of less than 100m) and preyed on the abundant bryozoans and other free-living taxa. However, stable primary production in the tropics allowed for diversification of prey species and this has caused many of modern tropical predatory gastropods to specialize on a narrow range of prey (Hughes, 1986). In our data this is evident in increases in the frequency of the predatory carnivorous family Conidae and increases in abundance in the family Turridae. The family Turridae are specialist feeders who feed on polychaetas, a suspension feeder whose populations are little affected by season changes in primary production (Hughes, 1986). The changing regime of primary production evidently has a great influence on the prey of predatory gastropods, for it is the depletion of most tropical families of predators that counts for the sharp drop in total number of species at the transition from tropical to temperate regimes (Hughes,1986). In our data this is evident from the decreases in the abundance of active predators and their replacement by browsing carnivores.

(ii) Herbivores

The tropical coasts of the Caribbean saw an increase in the number of herbivorous feeding categories over time. This is likely the result of the increase in coral reef and seagrass environments that would allow for a wider range of resources and wider range of suitable habitats to be available. For example, the herbivorous specimens in the older faunules (older than 3.5MA) are primarily feeders on fine-grained substrates. There are increases in the number of herbivorous specimens that primarily feed on, or include in their feeding habits: rock, rubble, coral or plant substrates. However, fine-grained, algal substrate environments didn't disappear entirely so there are still some specimens that feed solely on fine-grained or algal substrates in the younger faunules. The insignificance in changes of the distribution of herbivorous specimens may be due to the location of study. The diversity of non-predatory gastropods peaks between 40° and 60° latitudes where the climate favors the growth of attached algae (Hughes, 1986). This parallels our results as the increases in abundance of specimens that feed on rock, rubble and coral substrates was more significant than the increases seen in specimens that feed on plant or algae substrates. To determine the significance of changes in the individual Herbivorous feeding habits a Kruskal-Wallis test was made on the percent abundances of hard rock herbivores, soft substratum herbivores and plant/algal herbivores for the 3 age groups. It was found that the herbivores that are associated with rocky substratum were the only group of herbivores that saw a significant increase. This observation also coincides with research done on scallops in the area that shows an increase in byssally attached specimens (Smith and Jackson,2009).

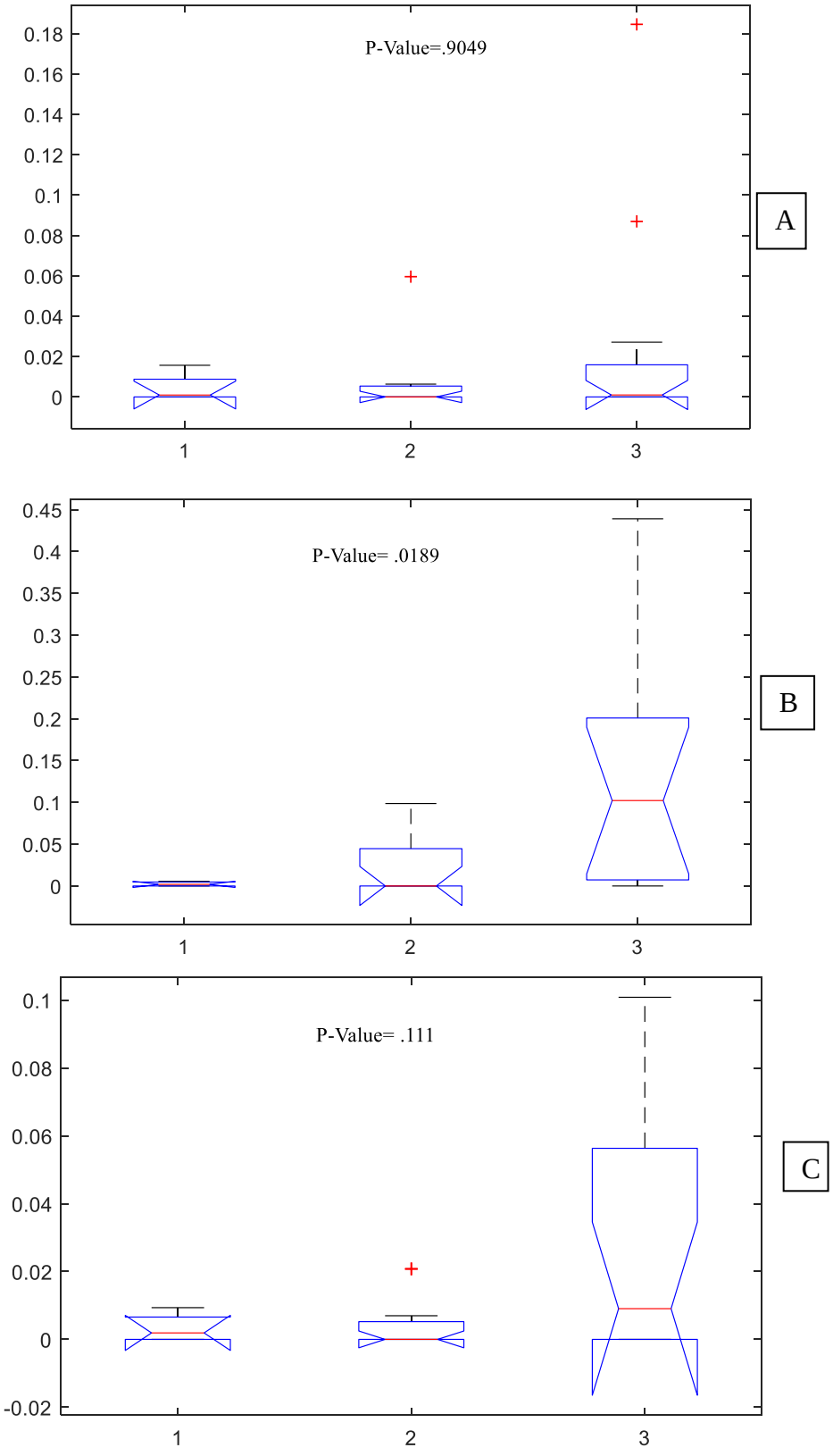

Figure 11-Shows the Kruskal-Wallis plots for A. Herbivores that feed on soft substratum B. Herbivores that feed on Rock, Coral or Rubble Substratum and C. Herbivores that feed on plant or algae for the age groups 1) Before 2) During and 3) After the formation of the Isthmus

(iii) *Omnivores*

The diversification of benthic habitats and resources would also explain the increase in the number of omnivorous feeding categories. For example, the omnivores in the older faunules are specimens that participate in predatory behaviors and behaviors that include feeding on plant algae or algae on soft substratum such as the family Xenophoridae. Xenophoridae specimens decreased in frequency and abundance in the younger faunules, which coincided with an increase in the number of omnivores that include in their diet sponges, cnidarians, corals or feed on rock and coral substrates such as the family Fissnrellidae. There is also a marked increase in the number of omnivores that feed on both sponges, cnidarians, corals and the algae that grow on the rock and coral substrates. This is consistent with increases in the abundance of Omnivorous specimens through time. Among the Omnivores group the Family Fissnrellidae, which participates in browsing carnivorous and hard rock herbivorous feeding habits, saw the largest increases in abundance. The increase in corals and associated rocky habitats likely facilitated the increase in Fissnrellidae abundance.

(iv) Suspension Feeders

After the closure of the Central American Seaway seagrass ecosystems shifted towards a more detritus-based ecology and there was an overall decrease in planktonic productivity (Leonard-Pingel et al., 2012). This brought about shallow seagrass meadows and rocky substrates associated with reef communities. Associated with the decrease in planktonic activity, the expectation for suspension activity in gastropods would be for a general decrease. This expectation is consistent with other research done on other Mollusks groups such as bivalves (Leonard-Pingel et al., 2012). In suspension feeding bivalves there is an overall decrease in the number of suspension feeding specimens due to decreases in suitable environments (Leonard-Pingel et al., 2012). However, the Turritellidae and Vermetridae families of suspension feeding gastropods prefer more sheltered locations and attach their shells to rocks or the undersides of rocky shores (Hughes, 1986). These types of environments increased after the closure of Central American Seaway. In contrast, the suspension feeding gastropod family Calyptraeoidea prefers to attach itself to soft, muddy substrates which were more prevalent before the closure of the Central American Seaway. The loss of muddy substrate environments was probably the main cause the Calyptraeoidea families decrease in frequency in the younger faunules. However, muddy substrate environments did not disappear entirely so suspension feeders that prefer the muddy substrate environments did not disappear entirely. The decrease in the Calyptraeoidea family coincides with increases in the frequency of members of the family Turritellidae and Vermetridae. This also coincides with an overall increase seen in the abundance of suspension feeding specimens in each faunule throughout time. The increase was likely caused by the increases in Vermetridae and Turritellidae communities.

Conclusions

The closure of the Central American Seaway and emergence of the Isthmus of Panama brought about major changes in ocean circulation patterns that affected the environmental conditions on either side of the land bridge. In the Caribbean a decrease in upwelling of deeper cooler water caused by isolation from El Nino events caused more stability in seasonal temperatures and productivity (O'Dea et al., 2007). The decrease in upwelling and changes in seasonal variations in temperature brought about an increase in coral reef communities. The increase of corals and other colonial species coupled with terrigenous runoff into the Caribbean has created an environment along tropical coasts of the Caribbean that is much more diverse than the Pacific coasts (O'Dea et al., 2007). The diversity of resources that are available allowed for an increase in the number of herbivorous and omnivorous feeding specimens while the feeding habits of the specimens reveal shifts towards diets that include the new resources of corals, sponges and rocky substrates. However, the distribution of herbivorous grazing gastropods may be constrained in this location due to unfavorable conditions for algae growth. The largest growth within the Herbivores group were the herbivores that preferentially feed on rock, coral and rubble substrates. The changing environment of the Caribbean also affected the suspension feeding gastropods which taxonomically shifted away from families that prefer to attach to muddy substrates and shifted towards families that prefer to attach to or under rocky surfaces. The Carnivorous group of gastropods were the most affected by the changes brought about by the formation of the Isthmus. There was an overall decrease in the abundance of carnivorous specimens, and furthermore, there was a shift in dominance away from predatory carnivores and towards browsing carnivores. Overall, taxonomic diversity doesn't change a significant amount rather there are shifts in the families that are present. The results indicate that the closure of the Central American Seaway and emergence of the Isthmus of Panama affected the various families of gastropods differently but overall increased the diversity of feeding habits and the number of different gastropod families in the area. These trends may be more difficult to see on the broad scale, but they can be seen when you consider the more specific life habits and feeding modes of the gastropod families in question.

Recommendations for Future Work

Future research on this topic may include higher order data analysis techniques to better compensate for natural variability seen in sample sizes for each faunule. Further analysis on the genus level of the specimen analyzed here would provide insight into the exact changes within the major families found in the study area. Further insight into the Turridae family may provide better insight into the changes that predatory gastropods experienced.

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Appendix

Family Names	Lennond	Swan Cay	Upper Lomas
Caecidae (HR/HP	2		
Acmaeidae (HR)	28		
Acteonidae (CP)			
Architectoniudae (CB)		6	
Buccinidae (CP)	2	41	2
Bullidae (HP)	3		17
Calyptraeidae (SU)	1	2	1
Cancellarioidea (CB)			
Cassidae (CP)			
Cavoliniidae (Holo)	1		
Cerithiidae (HP/HM/HR)	196		
Cerithiopsidae (CB)	1		
Columbellidae (CP)	59	10	
Conidae(CP)		9	44
Coralliophillidae (CB)	2		
Costellariidae (CP/CB)	1		
Cylichnidae (CP)			
Cypraeidae (HO)		12	
Cysticidae (CB)			1
Epitoniidae (CB)		10	1
Eratoidae (CB)	3		
Eulimoidea (CB)			
Fissnrellidae (HR/CB)	71	23	272
Haminoeidae (HP)			
Hipponicidae (HR/SU)			
Littorinidae (HR)			

Lottiidae (HR)	2		
Marginellidae (CB)		38	37
Mitridae (CP)	1		4
Modulidae (HR/HP)	70		
Muricidae (CP)	69	20	140
Nassariidae (CP)	41		88
Naticidae (CP)	3	13	
Neritidae (HO/HR)	20		
Olividae (CP)	1	99	603
Potamididae (HM)			
Pyramidelloidea (CB)	2		
Ranellidae (CP)	1		
Retusidae (CP)			
Rissoinidae (HP)	35		
Siliquariidae (SU)			10
Siphonariidae (HR/HP)			
Strombidae (HO)			
Terebridae (CP)			
Triphoridae (CB)	6		
Triviidae (CB)		1	
Trochidae (CB/HM)	6		2
Turbinidae (HR)	45		
Turridae (CP)	11	89	
Turritellidae (SU)	1	174	414
Vermetridae (SU)	55		
Vitrinellidae (HM/HP)			
Volutidae (CP)			
Xenophoridae (CP/Hm)		1	

Family Names	Empalme	Wild Cane Reef	Wild Cane Key
Caecidae (HR/HP			
Acmaeidae (HR)			2
Acteonidae (CP)			
Architectoniudae (CB)	31		1
Buccinidae (CP)	2		44
Bullidae (HP)	2		
Calyptraeidae (SU)	2		3
Cancellarioidea (CB)			
Cassidae (CP)			1
Cavoliniidae (Holo)			
Cerithiidae (HP/HM/HR)			9
Cerithiopsidae (CB)	5		1
Columbellidae (CP)	26		14
Conidae(CP)	35	2	7
Coralliophillidae (CB)	2		1
Costellariidae (CP/CB)			
Cylichnidae (CP)			
Cypraeidae (HO)			2
Cysticidae (CB)	30		2
Epitoniidae (CB)	5		
Eratoidae (CB)			
Eulimoidea (CB)	1		
Fissnrellidae (HR/CB)	146	1	14
Haminoeidae (HP)	1		
Hipponicidae (HR/SU)	1		2
Littorinidae (HR)	2		

Lottiidae (HR)			
Marginellidae (CB)	136	34	7
Mitridae (CP)			
Modulidae (HR/HP)			
Muricidae (CP)	66	30	10
Nassariidae (CP)	378	1	85
Naticidae (CP)	7	30	6
Neritidae (HO/HR)			
Olividae (CP)	196	110	18
Potamididae (HM)	2		
Pyramidelloidea (CB)	2		1
Ranellidae (CP)	1		
Retusidae (CP)			
Rissoinidae (HP)	12		4
Siliquariidae (SU)			
Siphonariidae (HR/HP)			4
Strombidae (HO)	2		
Terebridae (CP)	1		
Triphoridae (CB)	6		
Triviidae (CB)	82		2
Trochidae (CB/HM)	6		4
Turbinidae (HR)	15		
Turridae (CP)	172		21
Turritellidae (SU)	92	116	9
Vermetridae (SU)	4	5	22
Vitrinellidae (HM/HP)	2		
Volutidae (CP)	7		
Xenophoridae (CP/Hm)			

Family Names	Cemetery Pueblo	Ground Creek Porites	Ground Creek Mud
Caecidae (HR/HP			
Acmaeidae (HR)			
Acteonidae (CP)			
Architectoniudae (CB)			
Buccinidae (CP)			
Bullidae (HP)			110
Calyptraeidae (SU)			110
Cancellarioidea (CB)			2
Cassidae (CP)			
Cavoliniidae (Holo)			
Cerithiidae (HP/HM/HR)		22	
Cerithiopsidae (CB)			44
Columbellidae (CP)		28	1
Conidae(CP)	2	6	15
Coralliophillidae (CB)			
Costellariidae (CP/CB)			
Cylichnidae (CP)			
Cypraeidae (HO)			
Cysticidae (CB)			
Epitoniidae (CB)			14
Eratoidae (CB)			
Eulimoidea (CB)			
Fissnrellidae (HR/CB)	18	34	49
Haminoeidae (HP)			59
Hipponicidae (HR/SU)			
Littorinidae (HR)			15

Lottiidae (HR)			
Marginellidae (CB)			301
Mitridae (CP)		4	
Modulidae (HR/HP)			
Muricidae (CP)		29	27
Nassariidae (CP)		1	149
Naticidae (CP)			89
Neritidae (HO/HR)			216
Olividae (CP)		4	33
Potamididae (HM)			
Pyramidelloidea (CB)			5
Ranellidae (CP)			
Retusidae (CP)			8
Rissoinidae (HP)			2
Siliquariidae (SU)			
Siphonariidae (HR/HP)			
Strombidae (HO)			5
Terebridae (CP)			
Triphoridae (CB)			
Triviidae (CB)			
Trochidae (CB/HM)			3
Turbinidae (HR)			21
Turridae (CP)			121
Turritellidae (SU)	3	6	
Vermetridae (SU)		34	
Vitrinellidae (HM/HP)			2
Volutidae (CP)			
Xenophoridae (CP/Hm)			

Family Names	Fish Hole	Bomba	Quebrada	Santa Rita
Caecidae (HR/HP				
Acmaeidae (HR)				
Acteonidae (CP)				
Architectoniudae (CB)		22		
Buccinidae (CP)		1		
Bullidae (HP)		1	11	1
Calyptraeidae (SU)		3		
Cancellarioidea (CB)				
Cassidae (CP)		1		
Cavoliniidae (Holo)				
Cerithiidae (HP/HM/HR)				
Cerithiopsidae (CB)				
Columbellidae (CP)		167	24	
Conidae(CP)	31	8		
Coralliophillidae (CB)				
Costellariidae (CP/CB)		1		
Cylichnidae (CP)				
Cypraeidae (HO)		1		
Cysticidae (CB)				
Epitoniidae (CB)		4		
Eratoidae (CB)				
Eulimoidea (CB)		6		
Fissnrellidae (HR/CB)			3	3
Haminoeidae (HP)				
Hipponicidae (HR/SU)				
Littorinidae (HR)				

Lottiidae (HR)				
Marginellidae (CB)		69	8	
Mitridae (CP)		2		
Modulidae (HR/HP)				
Muricidae (CP)	2	7	4	9
Nassariidae (CP)		79	28	
Naticidae (CP)	36	129	27	22
Neritidae (HO/HR)				
Olividae (CP)	5	625	34	8
Potamididae (HM)				
Pyramidelloidea (CB)		17		
Ranellidae (CP)				
Retusidae (CP)		8		
Rissoinidae (HP)				
Siliquariidae (SU)				
Siphonariidae (HR/HP)				
Strombidae (HO)		10	4	
Terebridae (CP)		100		
Triphoridae (CB)				
Triviidae (CB)				
Trochidae (CB/HM)		1		
Turbinidae (HR)				
Turridae (CP)	111		2	
Turritellidae (SU)	23	30	111	2
Vermetridae (SU)		5		
Vitrinellidae (HM/HP)		1		
Volutidae (CP)			1	
Xenophoridae (CP/Hm)		1		

Family Names	Rio Vizcaya	Isla Solarte	Tiburon
Caecidae (HR/HP			
Acmaeidae (HR)			
Acteonidae (CP)			
Architectoniudae (CB)	1		
Buccinidae (CP)	4	6	
Bullidae (HP)			
Calyptraeidae (SU)	4		
Cancellarioidea (CB)			
Cassidae (CP)			
Cavoliniidae (Holo)			
Cerithiidae (HP/HM/HR)			
Cerithiopsidae (CB)			
Columbellidae (CP)	66	3	
Conidae(CP)	13	30	6
Coralliophillidae (CB)		2	
Costellariidae (CP/CB)			
Cylichnidae (CP)	3		
Cypraeidae (HO)		2	
Cysticidae (CB)			
Epitoniidae (CB)	15		
Eratoidae (CB)			
Eulimoidea (CB)	13		
Fissnrellidae (HR/CB)		46	
Haminoeidae (HP)			
Hipponicidae (HR/SU)			
Littorinidae (HR)			

Lottiidae (HR)			
Marginellidae (CB)	32	7	
Mitridae (CP)		1	
Modulidae (HR/HP)			
Muricidae (CP)	11	86	6
Nassariidae (CP)	2	11	
Naticidae (CP)	57	39	5
Neritidae (HO/HR)			
Olividae (CP)	677	148	36
Potamididae (HM)			
Pyramidelloidea (CB)			
Ranellidae (CP)			
Retusidae (CP)			
Rissoinidae (HP)			
Siliquariidae (SU)			
Siphonariidae (HR/HP)			
Strombidae (HO)			
Terebridae (CP)	54	2	
Triphoridae (CB)			
Triviidae (CB)			
Trochidae (CB/HM)			
Turbinidae (HR)		9	
Turridae (CP)	15	60	
Turritellidae (SU)	72	58	19
Vermetridae (SU)			
Vitrinellidae (HM/HP)			
Volutidae (CP)	1	1	
Xenophoridae (CP/Hm)		1	
Family Names	Nispero	Norte E	Norte W

Caecidae (HR/HP			
Acmaeidae (HR)			
Acteonidae (CP)			
Architectoniudae (CB)			
Buccinidae (CP)			
Bullidae (HP)			
Calyptraeidae (SU)			
Cancellarioidea (CB)			
Cassidae (CP)			
Cavoliniidae (Holo)			
Cerithiidae (HP/HM/HR)			
Cerithiopsidae (CB)			
Columbellidae (CP)			
Conidae(CP)	1	13	
Coralliophillidae (CB)			1
Costellariidae (CP/CB)			
Cylichnidae (CP)			
Cypraeidae (HO)			
Cysticidae (CB)			1
Epitoniidae (CB)			
Eratoidae (CB)			
Eulimoidea (CB)			1
Fissnrellidae (HR/CB)			
Haminoeidae (HP)			
Hipponicidae (HR/SU)			
Littorinidae (HR)			
Lottiidae (HR)			
Marginellidae (CB)			71

Mitridae (CP)			1
Modulidae (HR/HP)			
Muricidae (CP)	2	6	34
Nassariidae (CP)			24
Naticidae (CP)	13	26	18
Neritidae (HO/HR)			
Olividae (CP)	26	46	48
Potamididae (HM)			
Pyramidelloidea (CB)			
Ranellidae (CP)			
Retusidae (CP)			
Rissoinidae (HP)			
Siliquariidae (SU)			
Siphonariidae (HR/HP)			
Strombidae (HO)			3
Terebridae (CP)			2
Triphoridae (CB)			
Triviidae (CB)			
Trochidae (CB/HM)	1		6
Turbinidae (HR)			
Turridae (CP)	5		26
Turritellidae (SU)	149	8	51
Vermetridae (SU)			20
Vitrinellidae (HM/HP)			
Volutidae (CP)			
Xenophoridae (CP/Hm)	1		15
Family Names	Isla Popa	Roja W	Rio Tupisa
Caecidae (HR/HP			

Acmaeidae (HR)			
Acteonidae (CP)	1		
Architectoniudae (CB)		17	
Buccinidae (CP)			10
Bullidae (HP)		1	
Calyptraeidae (SU)		17	18
Cancellarioidea (CB)			1
Cassidae (CP)			
Cavoliniidae (Holo)			
Cerithiidae (HP/HM/HR)			1
Cerithiopsidae (CB)			
Columbellidae (CP)	9	2	77
Conidae(CP)	4	79	
Coralliophillidae (CB)			
Costellariidae (CP/CB)			
Cylichnidae (CP)		52	
Cypraeidae (HO)			
Cysticidae (CB)		62	
Epitoniidae (CB)	1	1	1
Eratoidae (CB)			
Eulimoidea (CB)	4		1
Fissnrellidae (HR/CB)		19	1
Haminoeidae (HP)		1	
Hipponicidae (HR/SU)		2	
Littorinidae (HR)			
Lottiidae (HR)		1	
Marginellidae (CB)	1	25	15
Mitridae (CP)		1	

Modulidae (HR/HP)		11	
Muricidae (CP)	6	48	10
Nassariidae (CP)	5	16	35
Naticidae (CP)	33	111	47
Neritidae (HO/HR)		11	
Olividae (CP)	12	748	25
Potamididae (HM)			
Pyramidelloidea (CB)		21	
Ranellidae (CP)			
Retusidae (CP)			
Rissoinidae (HP)			
Siliquariidae (SU)			
Siphonariidae (HR/HP)			
Strombidae (HO)		35	
Terebridae (CP)		22	2
Triphoridae (CB)			
Triviidae (CB)		2	
Trochidae (CB/HM)	2	7	2
Turbinidae (HR)		4	
Turridae (CP)		35	1
Turritellidae (SU)	5	163	14
Vermetridae (SU)	10		
Vitrinellidae (HM/HP)		13	
Volutidae (CP)			
Xenophoridae (CP/Hm)		10	
Family Names	Rio Indio	Mattress Fact	Isla Payardi
Caecidae (HR/HP			
Acmaeidae (HR)			

Acteonidae (CP)			1
Architectoniudae (CB)	3		10
Buccinidae (CP)	2		45
Bullidae (HP)			7
Calyptraeidae (SU)		4	43
Cancellarioidea (CB)	4		
Cassidae (CP)			
Cavoliniidae (Holo)			
Cerithiidae (HP/HM/HR)			
Cerithiopsidae (CB)			
Columbellidae (CP)	18		91
Conidae(CP)		11	4
Coralliophillidae (CB)			
Costellariidae (CP/CB)			
Cylichnidae (CP)			
Cypraeidae (HO)			
Cysticidae (CB)			
Epitoniidae (CB)	1		8
Eratoidae (CB)			
Eulimoidea (CB)			16
Fissnrellidae (HR/CB)			1
Haminoeidae (HP)			3
Hipponicidae (HR/SU)			
Littorinidae (HR)			
Lottiidae (HR)			
Marginellidae (CB)		1	42
Mitridae (CP)			
Modulidae (HR/HP)			

Muricidae (CP)	3	6	12
Nassariidae (CP)		1	452
Naticidae (CP)	35	16	573
Neritidae (HO/HR)			
Olividae (CP)	5	85	1430
Potamididae (HM)			
Pyramidelloidea (CB)			70
Ranellidae (CP)			
Retusidae (CP)			
Rissoinidae (HP)			
Siliquariidae (SU)			
Siphonariidae (HR/HP)			
Strombidae (HO)	1	6	2
Terebridae (CP)	11	1	136
Triphoridae (CB)			
Triviidae (CB)			
Trochidae (CB/HM)		4	
Turbinidae (HR)			
Turridae (CP)		3	97
Turritellidae (SU)		37	113
Vermetridae (SU)			
Vitrinellidae (HM/HP)			23
Volutidae (CP)			
Xenophoridae (CP/Hm)		5	